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Increased calf production in cattle selected for twin ovulations^{1,2}

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ABSTRACT: The effects of increasing fetal numbers and their distribution between the left and right uterine horns on calf survival, calf BW at birth and weaning, gestation length, dystocia, and calf sex ratio were evaluated for single ($n = 1,587$), twin ($n = 2,440$), and triplet calves ($n = 147$) born to primiparous and multiparous females in the Twinner population at the US Meat Animal Research Center between 1994 and 2004. Cattle were distributed equally between the spring and fall breeding seasons. Fetal number and distribution in utero were determined by real-time ultrasonography at 40 to 70 d postbreeding. For cows and heifers combined, number of calves per parturition increased from 1.34 in 1994 to 1.56 in 2004. Gestation length was 6.8 d shorter ($P < 0.01$) for twins compared with singles (277.5 ± 0.2 vs. 284.3 ± 0.2 d) and 12.7 d shorter for triplets (271.6 ± 0.8 d). Survival and BW of individual calves at birth decreased ($P < 0.01$) but total calf BW per dam increased ($P < 0.01$) as fetal number increased from single to triplet births. Twins resulting from bilateral twin ovulations had increased ($P < 0.01$) survival and BW at birth, a longer ($P < 0.01$) gestation length, and

less ($P < 0.01$) dystocia than twins resulting from unilateral twin ovulations. Calf survival and BW at birth were $97.2 \pm 0.3\%$ and 48.0 ± 0.1 kg for singles, $92.0 \pm 0.4\%$ and 39.0 ± 0.2 kg for bilateral twins, $83.2 \pm 0.4\%$ and 36.7 ± 0.2 kg for unilateral twins, $73.8 \pm 1.4\%$ and 30.6 ± 0.7 kg for bilateral triplets, and $51.9 \pm 3.2\%$ and 31.7 ± 1.6 kg for unilateral triplets. Birth weight of single calves increased by 0.51 kg/d for each additional day of gestation length vs. 0.38 kg/d for individual twins. Calf BW at birth increased ($P < 0.01$) with age of dam from 2 to 4 yr. Twin and triplet births had a greater ($P < 0.01$) incidence of dystocia than single births. The ratio of male:female calves (0.52:0.48) at birth was not affected by type of birth. Postnatal calf survival was similar for all 3 types of birth. Total progeny BW at weaning for single, twin, and triplet births was 217.7 ± 2.5 , 328.3 ± 3.2 , and 378.4 ± 15.0 kg, respectively ($P < 0.01$). Although most bovine females have the uterine capacity to gestate twin calves, decreased survival and BW of unilateral twins and of all triplets indicate that their growth and development may have been compromised by uterine crowding.

Key words: calf birth and weaning weight, cattle, fetal development, sex ratio, survival, twins

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INTRODUCTION

The production of twin births provides an opportunity to increase rate and efficiency of reproduction in beef cattle (Guerra-Martinez et al., 1990). However, reduced survival and BW of twin progeny at birth and weaning and an increased incidence of dystocia (Gregory et al.,

1996; Echternkamp and Gregory, 1999) compromise some of the potential economic gain from twinning in cattle. A long-term genetic selection program utilizing repeated records of ovulation rate in pubertal heifers, EBV estimated by multiple trait, repeated records analysis, and sires progeny tested for twinning increased the frequency of twin and triplet ovulations (Echternkamp et al., 1990; Van Vleck et al., 1991; Gregory et al., 1997). The consequence of this increase in ovulation rate has been an increased frequency of fraternal twin and triplet births to a combined annual rate of about 60%. Twin and triplet ovulations can occur either on the same ovary (i.e., unilaterally) or involve both ovaries (bilaterally). Migration of embryos between uterine horns is rare in cattle (Scanlon, 1972); thus, bovine embryos are gestated in the uterine horn adjacent to the ovary from which the oocyte(s) was ovulated (Echternkamp, 1992). Consequently, about half of the twin and triplet fetuses are contained within 1 uterine horn.

¹Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA.

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The effects of uterine space (i.e., twin conceptuses gestated in the same vs. separate uterine horns) on fetal survival and development, gestation length, dystocia, sex ratio, and postnatal growth are unknown, but cattle can gestate up to 3 fetuses within a uterine horn (Echternkamp, 1992). Because the frequency of triplet births is low in cattle (i.e., <0.1% of cattle births), little information is available regarding the performance of triplet calves.

The objective of this study was to assess the effects of fetal number and distribution in utero on gestation length, dystocia, sex ratio, survival, and performance of single, twin, and triplet calves.

MATERIALS AND METHODS

Animals and Experimental Design

Experimental design and procedures employed in this study were approved by the US Meat Animal Research Center (USMARC) Animal Care and Use Committee. The effect of maternal uterine environment on fetal development was evaluated on phenotypic records for 1,587 single, 2,440 twin, and 147 triplet calves born in the Twinner population at the USMARC between 1994 and 2004 to dams in which fetal numbers in the left and right uterine horn were determined by ultrasonography and the number of fetuses and calves born agreed. Gestation length was calculated for dams ($n = 1,211$) conceiving to AI. Assessment of the effect of type of birth on cow productivity included an additional 1,266 parturitions without ovulation rate measurements or with incorrect fetal data. Selection protocols, management procedures, and breed composition of the Twinner population have been reported previously (Echternkamp et al., 1990; Gregory et al., 1990, 1996). Herd size was reduced from 750 to 300 breeding females in 1997.

Approximately equal numbers of females were bred to calve in the spring and fall, with the spring breeding period (70 d) being from late May to early August and the fall period (60 d) from late October to late December. One-third of the females (i.e., females with the greatest EBV for twinning) were bred initially by AI over a 21-d period followed by natural service to young sires in individual sire breeding pastures (25 females/sire). The remaining two-thirds of the females were bred naturally to young sires in individual sire breeding pastures. Because of the measurement of ovulation rate in all yearling heifers (Echternkamp et al., 1990), nulliparous heifers were bred to produce their first calf at 2.5 yr of age. Number of calves born per parturition has increased from 1.34 in 1994 to 1.56 in 2004 (Echternkamp et al., 2007).

Animals were provided ad libitum access to grass pasture during the breeding periods, which was supplemented with corn silage (70%; DM basis) and alfalfa haylage (30%) during the fall breeding period. Females gestating, birthing, and nursing singles were fed a diet

of 70% haylage and 30% corn silage (DM basis) supplemented with alfalfa hay ad libitum pre- and postpartum to the beginning of breeding. Those diagnosed with twin or triplet fetuses were fed a higher energy diet (80% corn silage 17.5% high moisture corn, and 2.5% protein supplement; DM basis) beginning an average of 70 (spring) or 50 (fall) d before the beginning of the calving season; dams nursing twins continued to receive the higher energy diet postpartum. Diets, including supplemental diets, were fed at a rate to achieve a BCS of 5 to 6 on a scoring schedule of 1 to 9 (NRC, 1996), especially during the pre- and postpartum periods.

Cows were monitored frequently during the calving season for symptoms of dystocia. Dystocia was evaluated subjectively for each individual calf and assigned a descriptive score of 1 or 2 for no or little assistance by hand, 3 to 6 for increasing assistance with a calf jack, 7 for Caesarian birth, and 8 for abnormal fetal presentation (Echternkamp and Gregory, 1999). Parturitions receiving a score of 8 were given a second assistance score of 2 through 7 if assistance was required for extraction of the calf (Echternkamp and Gregory, 1999). Each twin and triplet calf was assigned a separate dystocia score.

All fully formed calves (i.e., alive or dead) were weighed individually within 24 h after birth. For triplet births with 3 live calves, the dam reared 2 calves and the third calf was cross-fostered to a dam whose calf had died. Feed was offered to the fall-born calves beginning at an average age of 30 d. Calves were weaned at an average age of 172 d; thus, spring-born calves were weaned in September and fall-born calves were weaned in February. Except for sire prospects, male calves were castrated at about 200 d of age using the band procedure.

Pregnancy Diagnosis

Beginning in 1994, ovulation rate [number of corpora lutea (CL)/ovary], pregnancy status, and fetal number and their distribution between the left and right uterine horns were determined after the spring and fall breeding season by real-time ultrasonography (Echternkamp and Gregory, 1999). Examinations were performed transrectally by scanning the uterus and both ovaries with a 3.5 MHz, convex-array probe (Aloka, Corometrics Medical Systems, Wallingford, CT) at approximately 70 d after the beginning of the breeding season. Females < 40 d of gestation or nonpregnant at the first examination were reexamined 35 to 40 d later. A technician proficient in diagnosing CL and fetal number collected all of the ovarian and fetal data. Pregnancy was reconfirmed by rectal palpation of the uterus at 75 to 135 d of gestation, and type of birth was recorded at calving.

Statistical Analysis

Effects of type of birth or fetal number and distribution in utero, age of dam, year of birth, season of birth,

sex of calf, and all possible 2-way interactions on calf survival and BW at birth and weaning, calf sex ratio, gestation length, dystocia, and cow productivity were analyzed by using PROC MIXED for repeated measures (SAS Inst. Inc., Cary, NC). Postnatal growth of twins is affected primarily by type of birth rather than type of rearing (Gregory et al., 1996), so type of rearing was not included in the model. Variables and interactions that were not significant ($P > 0.1$) were deleted from the final analyses. Any additional modifications to the statistical model are noted in the tables. Because the twin and triplet calves were of dizygotic and trizygotic origin, the effect of fetal number and implantation in the left vs. right uterine horn on fetal development was assessed for only those females in which the number of calves born equaled the number of CL detected on the ovaries. Fetal number and location were identified as single left, single right, unilateral twins left, unilateral twins right, bilateral twins, unilateral triplets, and bilateral triplets; data for unilateral triplets left or right were combined. Assessment of the effect of type of birth on cow productivity included additional females without the correct fetal information. Twin and triplet pregnancies composed of male and female calves were identified as mixed-sex pregnancies. Because growth traits did not differ between intact twin females and freemartin females born cotwin or cotriplet to a male(s), data for the 2 female groups were combined in the data analyses. Measurement of gestation length was limited to females conceiving to AI. Dystocia was subsequently categorized as absent (scores 1 or 2) or present (scores 3 through 8); the incidence (%) of dystocia was analyzed as 2 traits: 1) total incidence of dystocia and 2) incidence of abnormal fetal presentation (score 8). Because of the smaller number of triplet births, ANOVA were repeated using the same statistical models without triplets.

RESULTS

Gestation Length

For those females bred by AI, type of birth had a significant effect ($P < 0.01$) on gestation length, being 6.8 d shorter for twin (277.5 ± 0.2 d) and 12.7 d shorter for triplet (271.6 ± 0.8 d) births compared with single (284.3 ± 0.2 d) births. Gestation length (Table 1) was 1 d longer ($P < 0.05$) for bilateral twins compared with unilateral twins gestated in either the left or right uterine horn; the longer gestation length for bilateral than for unilateral triplets was not significantly different. Whether fetuses were gestated in the left or right uterine horn had no effect on gestation length. For single and twin pregnancies only (Table 2), the fetal number and location \times sex of calf interaction ($P < 0.01$) indicated a longer gestation length for single or same-sex bilateral twin pregnancies having male vs. female calves, but length did not differ between male vs. female same-sex unilateral twin pregnancies. Gestation length for twins of mixed sex was similar to that for female-female twins

but shorter ($P < 0.05$) than for male-male twins (Table 2). Overall, gestation length was 2 d shorter in the fall compared with the spring herd (Table 1), but the magnitude of this seasonal difference varied among years (year \times season; $P < 0.01$). The trend was for gestation length to decrease ($P < 0.01$) with year from 1994 (280.4 ± 0.3 d) to 2004 (278.3 ± 0.8 d). Age of dam did not influence gestation length.

Calf Survival at Birth and Weaning

Birth. Results for calf survival were computed for all fully formed calves with hair. Overall, calf survival at birth differed ($P < 0.01$) among single, twin, and triplet births; means for percentage of single, twin, and triplet calves alive at birth were 96.8 ± 0.5 , 88.6 ± 0.5 , and $69.7 \pm 2.7\%$, respectively. Results for the effects of fetal number and distribution between the left and right uterine horns on calf survival are reported in Table 1. Neonatal survival was greater for single than for twin calves regardless of whether the twins were gestated bilaterally ($P < 0.05$) or unilaterally ($P < 0.01$) within the uterus. However, calf survival was greater ($P < 0.01$) for bilateral than for unilateral twin or triplet pregnancies; calves from unilateral triplet pregnancies had the lowest ($P < 0.01$) survival. Comparisons of neonatal survival rates for only single and twin calves are presented in Table 2. Again, survival was similar among male and female single calves and female bilateral twins but greater than for unilateral twins (either sex) or for male bilateral twin calves (fetal number and location \times sex of calf; $P < 0.01$). Survival of single or unilateral twin calves was not affected by being gestated in the left vs. right uterine horn (Table 2). Age of dam did not have a consistent effect on neonatal calf survival. Survival was greater ($P < 0.01$) for calves born in the spring than in the fall for most, but not all, years (year \times season; $P < 0.05$). Occurrence of dystocia had no effect on the survival of single or triplet calves, but twin-born calves with dystocia had a lower survival rate than those without dystocia (type of birth \times dystocia; $P < 0.01$). Number of live twin and triplet calves per parturition (Table 3) also varied among ages of dams, but number of live single calves was not affected by age of dam (type of birth \times age of dam; $P < 0.01$).

Weaning. Survival from birth to weaning was similar among calves from the 3 types of birth, ranging between 87 and 90% in most years. Percentage of progeny weaned (Table 1) was influenced by those factors (i.e., type of birth and season) affecting survival at birth. Percentage of progeny weaned was greatest for singles, intermediate for twins, and least for triplets (88.8 ± 0.9 vs. 78.4 ± 0.7 vs. $59.6 \pm 3.1\%$, respectively; $P < 0.01$). The percentage of twin calves weaned from bilateral twin pregnancies (especially female twins) was similar to single calves but greater ($P < 0.01$) than for those from unilateral twin pregnancies. Bilateral triplet pregnancies also weaned a greater ($P < 0.01$) percentage of calves than unilateral triplet pregnancies and had a

Table 1. Effects of fetal number and location in utero and of season on least squares means for gestation length and for survival and BW of calves at birth and weaning

Item	No. of cows	Gestation length, d	No. of calves	Calf survival, %		Calf BW, kg	
				Birth	Weaning	Birth	Weaning
Fetal number and location							
1 Left	300	284.5 ± 0.2 ^a	711	97.3 ± 1.1 ^{ae}	87.6 ± 1.5 ^a	48.0 ± 0.2 ^a	257.1 ± 1.1 ^a
1 Right	360	284.2 ± 0.2 ^a	876	97.0 ± 1.0 ^{ae}	88.3 ± 1.3 ^a	47.9 ± 0.2 ^a	258.6 ± 1.0 ^a
2 Left	96	277.2 ± 0.2 ^{bce}	446	83.6 ± 1.4 ^b	70.7 ± 1.9 ^b	36.8 ± 0.3 ^b	220.6 ± 1.6 ^b
2 Right	167	277.0 ± 0.1 ^b	838	82.7 ± 1.0 ^b	73.2 ± 1.4 ^b	36.6 ± 0.2 ^b	222.0 ± 1.1 ^b
2 Bilateral	259	278.2 ± 0.1 ^{cf}	1,158	94.0 ± 0.9 ^{af}	85.4 ± 1.2 ^a	39.0 ± 0.2 ^c	222.1 ± 0.9 ^b
3 Unilateral	5	271.0 ± 0.8 ^d	27	51.9 ± 7.1 ^c	40.7 ± 9.6 ^c	31.7 ± 1.6 ^d	217.1 ± 14.3 ^{bc}
3 Bilateral	24	273.8 ± 0.3 ^d	120	73.8 ± 3.1 ^d	63.9 ± 4.2 ^b	30.6 ± 0.7 ^d	199.9 ± 4.0 ^c
Season							
Spring	702	280.7 ± 0.2 ^a	2,165	93.3 ± 1.2 ^a	84.6 ± 1.8 ^a	39.3 ± 0.4 ^a	226.3 ± 2.2 ^a
Fall	509	278.6 ± 0.2 ^b	2,011	88.6 ± 1.2 ^b	78.5 ± 1.7 ^b	38.3 ± 0.3 ^b	229.5 ± 2.2 ^b

^{a-d}Means (± SEM) without a common superscript differ within an item; $P < 0.01$.

^{e,f}Means (± SEM) without a common superscript differ within an item; $P < 0.05$.

percentage similar to unilateral twins. In comparisons limited to single and twin calves (Table 2), male calves from a single or unilateral twin pregnancy in the left, but not right, uterine horn or from a bilateral twin pregnancy had a lower survival rate to weaning than contemporary female calves (fetal number and location × sex of calf; $P < 0.01$). The seasonal effect on calf survival to weaning varied among years (year × season; $P < 0.01$), but overall, survival was greater ($P < 0.01$) for spring-born calves than for fall-born calves. Age of dam did not affect calf survival to weaning.

Calf BW

Birth. Birth weight of the individual calves decreased ($P < 0.01$) as fetal number in utero increased from 1 to 2 to 3 (Table 1). Conversely, total calf BW per dam (Table 3) increased ($P < 0.01$) from single to triplet births. Twin calves gestated in separate uterine horns were heavier ($P < 0.01$) at birth than twins gestated in 1 horn, whereas BW of triplets did not differ between bilateral and unilateral pregnancies. Analysis of data for only single and twin calves (Table 2) revealed that

Table 2. Effects of fetal number and location in utero, age of dam, sex of calf, season, and year on least squares means for gestation length and for survival and BW of single and twin calves at birth and weaning

Item	No. of cows	Gestation length, d	No. of calves	Calf survival, %		Calf BW, kg	
				Birth	Weaning	Birth	Weaning
Age of dam, yr							
2	253	279.6 ± 0.3	1,189	91.2 ± 0.9	82.0 ± 0.9	38.6 ± 0.2 ^a	222.1 ± 0.9 ^a
3	306	280.0 ± 0.4	938	88.7 ± 1.0	78.5 ± 1.0	41.1 ± 0.2 ^b	235.5 ± 1.1 ^b
4	226	279.1 ± 0.4	736	90.7 ± 1.1	81.3 ± 1.1	42.7 ± 0.3 ^c	241.9 ± 1.2 ^c
5	165	279.1 ± 0.5	492	90.4 ± 1.4	81.0 ± 1.4	43.3 ± 0.3 ^{cd}	241.8 ± 1.4 ^c
≥6	232	280.5 ± 0.5	674	92.6 ± 1.1	83.5 ± 1.1	43.6 ± 0.3 ^d	240.6 ± 1.2 ^c
Season							
Spring	690	284.5 ± 0.6 ^a	2,109	92.7 ± 0.7 ^a	84.2 ± 0.7 ^a	42.2 ± 0.1 ^a	234.6 ± 0.8 ^a
Fall	492	282.8 ± 0.6 ^a	1,920	88.7 ± 0.7 ^b	78.4 ± 0.9 ^b	41.5 ± 0.2 ^b	238.1 ± 0.8 ^b
Fetal number and location × sex of calf							
1 Left Male	170	284.5 ± 0.6 ^a	367	96.3 ± 1.6 ^{af}	84.1 ± 2.0 ^{aef}	49.7 ± 0.4 ^a	267.0 ± 1.8 ^a
1 Left Female	130	282.8 ± 0.6 ^b	344	97.8 ± 1.6 ^a	90.9 ± 2.0 ^b	45.8 ± 0.4 ^b	249.7 ± 1.8 ^b
1 Right Male	201	283.4 ± 0.6 ^{ab}	481	96.7 ± 1.4 ^a	86.6 ± 1.8 ^{ab}	50.4 ± 0.3 ^a	267.1 ± 1.5 ^a
1 Right Female	159	282.1 ± 0.6 ^b	395	96.9 ± 1.5 ^a	89.8 ± 1.9 ^{abg}	46.4 ± 0.3 ^b	252.5 ± 1.6 ^b
2 Left Male	28	276.3 ± 0.7 ^{cef}	234	80.9 ± 1.8 ^b	65.3 ± 2.3 ^c	38.0 ± 0.5 ^c	227.4 ± 2.1 ^c
2 Left Female	26	277.8 ± 0.8 ^{cde}	212	82.0 ± 1.8 ^b	73.3 ± 2.4 ^d	36.6 ± 0.5 ^{ce}	212.8 ± 2.2 ^d
2 Left Mixed	42	275.9 ± 0.7 ^{ef}					
2 Right Male	47	278.1 ± 0.5 ^{egh}	428	85.5 ± 1.5 ^{bch}	75.3 ± 1.9 ^d	37.5 ± 0.3 ^c	227.3 ± 1.6 ^c
2 Right Female	48	277.1 ± 0.5 ^{ce}	410	86.3 ± 1.5 ^{bch}	79.5 ± 1.9 ^{dh}	36.7 ± 0.3 ^{ce}	215.5 ± 1.6 ^d
2 Right Mixed	72	276.2 ± 0.5 ^{ef}					
2 Bilateral Male	63	279.1 ± 0.5 ^d	600	91.0 ± 1.2 ^{cdg}	79.6 ± 1.4 ^{de}	40.2 ± 0.2 ^d	226.1 ± 1.3 ^c
2 Bilateral Female	72	277.4 ± 0.5 ^{ce}	558	95.7 ± 1.3 ^{adf}	89.1 ± 1.5 ^{ab}	38.1 ± 0.2 ^{cf}	218.9 ± 1.4 ^d
2 Bilateral Mixed	124	277.7 ± 0.4 ^{ceg}					

^{a-e}Means (± SEM) without a common superscript differ; $P < 0.01$.

^{f-h}Means (± SEM) without a common superscript differ; $P < 0.05$.

Table 3. Comparison of total live calf production at birth and weaning among dams producing single, twin, and triplet births as affected by age of dam

Type of birth	Age of dam, yr	n	Live calves/parturition	Total live calf BW/parturition, ¹ kg	Total weaning BW/parturition, ² kg
Single	2	788	0.95 ± 0.02 ^a	42.8 ± 0.4 ^a	211.8 ± 4.4 ^a
	3	607	0.94 ± 0.02 ^a	45.4 ± 0.4 ^b	214.5 ± 5.1 ^a
	4	390	0.96 ± 0.02 ^a	49.8 ± 0.5 ^c	223.1 ± 6.4 ^a
	5	293	0.95 ± 0.03 ^a	47.8 ± 0.6 ^d	206.6 ± 7.3 ^a
	≥6	463	0.96 ± 0.02 ^a	48.7 ± 0.5 ^{cd}	225.8 ± 5.8 ^a
Twin	2	422	1.75 ± 0.02 ^b	60.3 ± 0.5 ^e	322.4 ± 6.1 ^{bj}
	3	365	1.65 ± 0.02 ^c	60.3 ± 0.5 ^e	322.0 ± 6.5 ^{bj}
	4	302	1.63 ± 0.03 ^{cj}	62.6 ± 0.6 ^{fi}	326.0 ± 7.2 ^b
	5	180	1.72 ± 0.03 ^{bck}	68.4 ± 0.8 ^{gk}	339.4 ± 9.3 ^b
	≥6	243	1.66 ± 0.03 ^c	64.9 ± 0.7 ^h	331.5 ± 8.0 ^b
Triplet	2	17	2.08 ± 0.12 ^d	53.4 ± 2.5 ^{cdel}	339.0 ± 30.5 ^b
	3	17	1.95 ± 0.12 ^{bd}	58.3 ± 2.5 ^{efhl}	354.0 ± 30.5 ^b
	4	12	2.82 ± 0.13 ^e	90.4 ± 2.9 ⁱ	493.1 ± 35.6 ^c
	5	9	2.17 ± 0.15 ^d	68.9 ± 3.4 ^{ghk}	427.8 ± 41.8 ^{bck}
	≥6	15	1.89 ± 0.12 ^{bcdk}	62.0 ± 2.7 ^{efgh}	399.3 ± 34.1 ^{bjk}

^{a-i}Means without a common superscript differ within a column; $P < 0.01$.

^{j-l}Means without a common superscript differ within a column; $P < 0.05$.

¹Total BW of live calf or calves at birth per cow calving; least-squares means ± SEM.

²Total BW of calf or calves weaned per cow calving; least-squares means ± SEM.

BW of male calves from single or bilateral twin births were heavier at birth than contemporary female calves, whereas sex of calf did not affect BW of unilateral twins (fetal number and location × sex of calf; $P < 0.01$). Also, female calves from bilateral twin pregnancies were lighter ($P < 0.01$) at birth than single females but were heavier ($P < 0.05$) than females from unilateral twin pregnancies. Neonatal calf BW increased with increasing age of the dam, but the effect of age of dam on calf BW did vary among years (age of dam × year; $P < 0.01$). Single and twin calves of 3-yr-old dams were heavier ($P < 0.01$) at birth than calves of 2-yr-old dams but lighter ($P < 0.01$) than those of older dams (Table 2). Likewise, the trend was for spring-born calves to be heavier than fall-born calves but not in all years (year × season; $P < 0.01$). For single and twin births, cows producing calves with heavier ($P < 0.01$) BW had a greater incidence of dystocia (Table 4).

Figure 1 illustrates the relationship between gestation length and calf BW at birth for single- vs. twin-born calves. Birth weight increased linearly ($P < 0.01$) during the normal range for gestation length, but the slope of the regression was less for twins compared with singles ($P < 0.01$). Thus, single calves were heavier than individual twin calves by 5.4 kg at 270 d of gestation and by 8.3 kg at 290 d.

Weaning. At weaning, progeny BW was affected ($P < 0.01$) by fetal number and location in utero, sex of calf, season, year of birth, age of dam, and their interactions. The effect of fetal number and location on BW of individual calves at weaning (Table 1) exhibited the same trend ($P < 0.01$) as at birth with 2 exceptions: 1) BW did not differ between twins gestated bilaterally vs. unilaterally and 2) fall-born calves were generally heavier than spring-born calves. Individual twin and

triplet calves were lighter ($P < 0.01$) than single calves (Table 1) and bilateral triplets were lighter ($P < 0.01$) than twins at weaning, but BW did not differ among bilateral twins, unilateral twins, and unilateral triplets at weaning (type of birth × location; $P < 0.01$). For single and twin calves only, BW at weaning increased ($P < 0.01$) with age of dam from 2 to 3 to 4 yr of age (Table 2). The trend for fall-born calves to be heavier than spring-born calves at weaning (Table 2) was not detected in all years (season × year; $P < 0.01$).

Cow Productivity

Although survival of individual calves decreased as type of birth changed from single to triplets, the total

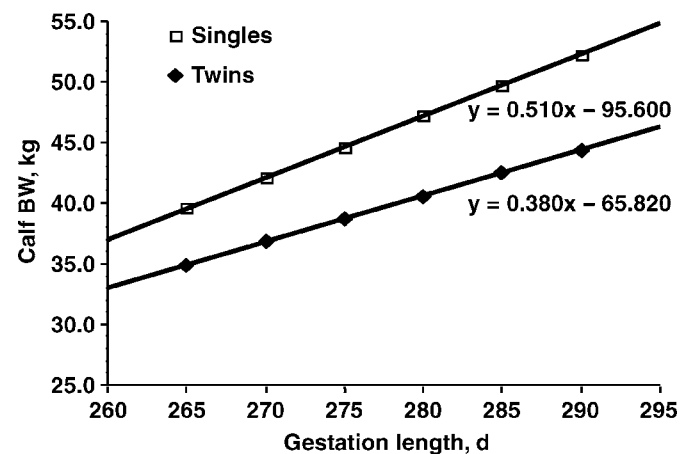


Figure 1. Relationships between calf BW at birth and length of gestation for individual single- (□) and twin- (◆) born calves. Slope of the regression line differed ($P < 0.01$) between single- and twin-born calves.

Table 4. Relationship between dystocia and calf survival or BW at birth¹

Type of birth	Dystocia	No. of parturitions	Live calves/parturition	Total calf BW/parturition, kg
Single	No	1,965	0.97 ± 0.01 ^a	46.9 ± 0.2 ^a
	Yes	576	0.93 ± 0.02 ^a	51.9 ± 0.4 ^b
Twin	No	960	1.77 ± 0.01 ^b	72.2 ± 0.3 ^c
	Yes	552	1.60 ± 0.01 ^c	78.6 ± 0.5 ^d
Triplet	No	15	2.21 ± 0.12 ^d	89.3 ± 2.7 ^e
	Yes	55	2.16 ± 0.06 ^d	93.5 ± 1.4 ^e

^{a-e}Means within a column without a common superscript differ; $P < 0.01$.

¹Dystocia was associated with delivery of 1 or more calves. Least squares means ± SEM.

number of live calves per parturition still increased (Table 3). Age of dam did not affect survival of single calves, whereas survival of twin and triplet calves varied significantly among ages but in no consistent pattern (type of birth × age of dam; $P < 0.01$). The occurrence of dystocia (Table 4) reduced survival of single and twin calves at birth but dystocia did not affect survival of triplet calves (type of birth × dystocia; $P < 0.01$). Total BW of live progeny at birth (Table 3) or of all progeny at birth (Table 4) was affected ($P < 0.01$) by type of birth, increasing from single to triplet births; this difference in total calf BW was greater for all progeny compared with only live progeny. The effect of age of dam on total BW of live progeny at birth (Table 3) varied among the 3 birth groups (type of birth × age of dam; $P < 0.01$). Progeny from first-parity dams (2 yr old) had the lightest total BW at birth (Table 3), and total live calf BW increased ($P < 0.01$) with age of dam from 2 to 4 yr of age for single births and from 2 to 5 yr of age for twin births. The effect of age of dam on progeny BW was variable for dams ≥ 4 yr of age. Total progeny BW at weaning per parturition also differed ($P < 0.01$) among single, twin, and triplet births (217.7 ± 2.5, 328.3 ± 3.2, 378.4 ± 15.0 kg, respectively). For triplets, total progeny BW (Table 3) varied among ages of dams (type of birth × age of dam; $P < 0.01$); dams 4 and 5 yr of age producing triplets weaned the most progeny BW.

Dystocia

Total. The increased ($P < 0.01$) incidence of dystocia for twin or triplet births compared with single births (Table 4) resulted primarily from abnormal presentation of 1 or both twins at delivery compared with dystocia for singles requiring hand or mechanical assistance to deliver the calf (Table 5). Single and twin calves with dystocia were heavier ($P < 0.01$) at birth compared with calves without dystocia (Table 4), whereas birth weight of triplets did not differ between those with or without dystocia. Because of missing subgroups for triplet births, dystocia data were subsequently evaluated

Table 5. Effect of fetal number and location in utero on incidence of dystocia

Type of birth	Uterine horn location	n	Dystocia ¹	
			Total, %	Malpresentations, %
Single	Left	711	25.1 ± 1.8 ^a	4.8 ± 1.6 ^a
	Right	876	20.3 ± 1.6 ^a	6.0 ± 1.5 ^a
Twin	Left	446	58.1 ± 2.3 ^{be}	50.8 ± 2.0 ^{be}
	Right	838	57.6 ± 1.6 ^{be}	45.6 ± 1.5 ^{bf}
Triplet	Bilateral	1,158	49.8 ± 1.4 ^c	33.6 ± 1.3 ^c
	Unilateral	27	62.7 ± 11.7 ^{bc}	62.7 ± 10.3 ^{bcd}
	Bilateral	120	70.4 ± 5.1 ^{bf}	70.4 ± 4.7 ^d

^{a-d}Means within a column without a common superscript differ; $P < 0.01$.

^{e,f}Means within a column without a common superscript differ; $P < 0.05$.

¹Total incidence of dystocia or incidence of dystocia associated with malpresentation for individual calves; number of calves born equaled number of ovulation. Least squares means ± SEM.

for only single and twin births (Table 6). Males from single and same-sex twin births had a greater incidence of dystocia than female births, an exception being left unilateral twins (type of birth × sex of calf; $P < 0.01$). Unilateral twin births had a greater incidence of dystocia in the spring than in the fall, but single left had a lower incidence in the spring; the incidence did not differ between seasons for single right or bilateral twin births (fetal number and location × season; $P < 0.01$). First parity dams (i.e., 2-yr-old dams) had a greater incidence of dystocia than dams ≥ 3 yr of age (Table 6).

Malpresentation. An assessment of factors contributing to the increased incidence of malpresentation for twin compared with single births is presented in Table 6. The incidence of malpresentation was less ($P < 0.01$) for singles compared with twins and did not differ between fetuses in the left vs. right uterine horn (4.8 vs. 6.0%, respectively). Conversely, the increased incidence with twins did differ ($P < 0.01$) by location within the uterus: bilateral twins, 33.6%; unilateral twins right, 45.7%; and unilateral twins left, 50.8%. The incidence of malpresentation increased ($P < 0.01$) with age of dam, being greater in dams ≥ 6 yr of age. Season did not affect the incidence of malpresentation, but the incidence was greater ($P < 0.01$) in 2000 and 2001 compared with the other years.

Calf Sex Ratio

Ratios of male:female calves at birth are presented in Table 7 for both single- and twin-born calves. The overall ratio of male:female calves at birth was 0.52:0.48, and the sex ratio did not differ between single and twin births. Thus, conceptus gender did not affect survival of single or twin conceptuses in utero, including twin pairs that were of the same sex or of mixed sex within 1 uterine horn.

DISCUSSION

Continued selection for an increased frequency of twin ovulations and births continues to increase the

Table 6. Influence of fetal number and location in utero on the incidence of dystocia and their interactions with sex of calf, season, and age of dam for dams producing single or twin births¹

Item		n	Total, %	Malpresentations, %
Fetal number and location				
1 Left		711	25.3 ± 1.8 ^{af}	4.8 ± 1.6 ^a
1 Right		876	20.7 ± 1.7 ^{ag}	6.0 ± 1.5 ^a
2 Left		446	58.4 ± 2.3 ^b	50.8 ± 2.0 ^{bf}
2 Right		838	57.9 ± 1.7 ^b	45.6 ± 1.5 ^{bg}
2 Bilateral		1,158	49.9 ± 1.5 ^c	33.6 ± 1.3 ^c
Fetal number and location × sex of calf				
1 Left	Male	367	32.5 ± 2.6 ^a	5.9 ± 2.1 ^a
	Female	344	18.2 ± 2.5 ^b	3.7 ± 2.2 ^a
1 Right	Male	481	26.7 ± 2.2 ^a	6.1 ± 1.9 ^a
	Female	395	14.6 ± 2.4 ^b	5.9 ± 2.1 ^a
2 Left	Male	130	53.6 ± 4.0 ^{efj}	44.4 ± 3.5 ^b
	Female	108	63.2 ± 4.4 ^{efg}	57.9 ± 3.9 ^{ef}
	Mixed	208	58.3 ± 3.3 ^c	50.3 ± 2.8 ^{befh}
2 Right	Male	238	63.1 ± 3.0 ^{eg}	49.0 ± 2.6 ^{begh}
	Female	220	52.8 ± 3.1 ^{cehj}	42.6 ± 2.7 ^{bg}
	Mixed	380	57.7 ± 2.4 ^c	45.5 ± 2.1 ^b
2 Bilateral	Male	326	62.8 ± 2.6 ^{cg}	42.8 ± 2.2 ^{bg}
	Female	284	40.2 ± 2.7 ^{di}	26.6 ± 2.4 ^d
	Mixed	548	46.7 ± 2.0 ^{dej}	31.3 ± 1.7 ^d
Fetal number and location × season				
1 Left	Spring	406	21.8 ± 2.4 ^{abf}	
	Fall	305	28.9 ± 2.8 ^{bg}	
1 Right	Spring	522	18.6 ± 2.1 ^a	
	Fall	354	22.8 ± 2.6 ^{ab}	
2 Left	Spring	216	65.2 ± 3.2 ^c	
	Fall	230	51.6 ± 3.2 ^d	
2 Right	Spring	368	62.1 ± 2.5 ^c	
	Fall	470	53.6 ± 2.2 ^d	
2 Bilateral	Spring	596	51.8 ± 2.0 ^d	
	Fall	562	48.1 ± 2.0 ^d	
Age of dam, yr				
2		1,190	49.3 ± 1.5 ^{af}	24.8 ± 1.3 ^a
3		939	41.7 ± 1.7 ^b	25.7 ± 1.5 ^a
4		735	39.2 ± 1.9 ^b	27.9 ± 1.6 ^a
5		492	38.0 ± 2.3 ^{bg}	28.8 ± 2.0 ^{abf}
≥6		670	43.9 ± 1.9 ^{abh}	33.7 ± 1.7 ^{bg}

^{a-e}Means within a column and variable without a common superscript differ; $P < 0.01$.^{f-j}Means within a column and variable without a common superscript differ; $P < 0.05$.¹Least squares means ± SEM.

frequency of twin births and more recently the frequency of triplet ovulations and births in the Twinner population at the USMARC. The current study evaluated the effects of fetal number and distribution within the uterus and of uterine capacity on prenatal growth and birth weight, neonatal survival, gestation length, incidence of dystocia, and the sex ratio of male to female calves for single, twin, and triplet births. Although most bovine females have the uterine capacity to gestate twin fetuses to term, twin fetuses gestated in separate uterine horns (bilateral twins) had greater neonatal survival, heavier birth weight (especially males), and a longer gestation length than twins gestated in 1 uterine horn. Calf survival was also greater for bilateral vs. unilateral triplets. Thus, the additional uterine space for bilateral twin and triplet fetuses appeared to improve fetal development, providing possible evidence of maternal uterine or placental restrictions on the growth

of twin and triplet fetuses. The incidence of fetal abortions was also increased in dams gestating triplets, especially first parity dams (Echternkamp et al., 2007), and total calf BW at birth increased with age of dam; further possible evidence of a maternal uterine influence on fetal growth, especially with twins and triplets. Survival and BW did not differ between single calves or unilateral twin calves gestated in the left vs. right uterine horn, indicating that maternal uterine environment was the same for both uterine horns.

Concentrations of pregnancy-associated glycoproteins were also found to be greater in the blood of dams with bilateral vs. unilateral twin pregnancies (Echternkamp et al., 2006b), indicating that the heavier BW of bilateral twin calves was likely associated with increased placental mass. Ferrell and Reynolds (1992) reported that total uterine blood flow and nutrient uptake were greater in cows gestating twin fetuses vs. a

Table 7. Influence of fetal number and location in utero on sex of calf for single and twin births

Fetal number and location	No. of calves	Sex of calf	
		Male	Female ¹
1 Left	711	0.516	0.484
1 Right	876	0.549	0.451
2 Left	446	0.525	0.475
2 Right	838	0.511	0.489
2 Bilateral	1,158	0.518	0.482

¹Fertile and freemartin females combined.

single fetus, but did not differentiate uterine blood flow and nutrient uptake between bilateral and unilateral twin pregnancies. However, uterine and umbilical blood flow and oxygen and nutrient uptake per fetus were found to be about 25% less for twins compared with a single fetus, which is consistent with a smaller growth rate in utero for twin vs. single fetuses. For example, birth weight increased 0.51 kg for each additional day of gestation for singles compared with 0.38 kg/d for twin fetuses. An assessment of genetic variation for birth weight between single and twin calves yielded heritability estimates of 0.50 and 0.33 for birth weight of individual single and twin calves, respectively (Allan et al., 2007). However, estimates of permanent environmental variance were significantly greater in the twin birth weight data compared with single birth data, which may also indicate potential limitations in uterine environment (e.g., capacity or placental function) for twin pregnancies among dams. Although birth weight does increase with gestation length, the additional 7 d in gestation length for single vs. twin calves and the 1-d difference between bilateral and unilateral twins can only account for a small portion of the difference in birth weight between twins and singles.

In cattle, the right ovary has a greater frequency of ovulations than the left ovary, and this difference in activity is also found in twin-ovulating cattle (Echternkamp et al., 1990; Echternkamp and Gregory, 2002). Migration of embryos between uterine horns is rare in cattle (Scanlon, 1972; Echternkamp, 1992) and, thus, the greater frequency of singles and unilateral twins gestated in the right than left uterine horn. Because of the increased survival of bilateral twin calves, approaches to increase the proportion of bilateral twin ovulations should enhance production gains from a twinning technology (Echternkamp and Gregory, 2002; Cushman et al., 2005).

Survival of the calves from birth to weaning was similar among the 3 birth groups; thus, differences among birth groups in progeny survival at weaning reflected differences in calf survival at birth. Likewise, trends in BW at weaning among singles, twins, and triplets were similar to those at birth, except the uterine effect on BW of bilateral vs. unilateral twins detected at birth was compensated for postnatally and was not found at weaning. However, occurrence of postnatal compensa-

tory growth in twin and triplet calves relative to singles was negligible in this management system even though milk production is enhanced in the Twinner population from the inclusion of dairy animals in the foundation herd. These results concur with previous findings that postnatal growth of twins is affected primarily by type of birth rather than type of rearing (Gregory et al., 1996). To increase postnatal survival and growth of triplet calves, the USMARC protocol is to cross-foster 1 of the 3 live calves to a surrogate dam. Twenty percent of the triplet calves were cross-fostered to a surrogate dam and reared as a single. Weaning BW of the fostered triplet calves was 2 to 3% heavier than for triplets reared as twins, further indicating that postnatal growth of twins and triplets is primarily impacted by type of birth. The increased weaning BW for the fall-born calves likely reflected the benefit of creep feeding fall-born calves and increased milk production by their dams from the increased dietary energy.

Overall effects of season and year on calf survival and BW and on gestation length reflected seasonal and year differences in ovulation and twinning rate and the negative effects of twin and triplet births on fetal growth and calf survival. Ovulation rate, and consequently twinning rate, is greater in the fall than in the spring breeding and calving seasons; thus, overall means for calf survival and BW and for length of gestation were less in the fall compared with the spring. Alternatively, because ambient temperatures, and likely maternal body temperatures, were elevated during the third trimester of pregnancy (i.e., July to August) in fall-calving cows, the decreased birth weight of individual fall-born calves may be a consequence of heat stress and the associated diversion of blood flow from the uterus to peripheral tissues (Reynolds et al., 1985). Likewise, selection for increased ovulation and twinning rate continues to increase the frequency of twin and triplet births in this population; thus, accounting for the decrease in overall means for calf survival and BW and for gestation length from 1994 to 2004. As reported previously (Gregory et al., 1996), birth and weaning BW did not differ statistically between freemartin and intact twin females and, thus, BW data for the 2 groups were combined. However, results from the previous study did show differences in muscle development, fat deposition and carcass traits for the freemartin.

Gestation length decreased as number of calves within the pregnancy increased. The shorter gestation length for twins and triplets is likely the effect of uterine crowding associated with the additional fetus(es). Gestation length was also shorter for female than for male calves in both single and same-sex twin pregnancies; mixed-sex twin pregnancies had a shorter gestation length similar to female-female twins. Results from reciprocal-cross ovine pregnancies created by embryo transfer indicated that breed of embryo rather than breed of recipient (Anderson et al., 1981) determined gestation length; thus, gestation length of mixed-sex

twins reflected the shorter gestation length of the female calf.

Twin and triplet births increased the frequency of dystocia as a result of abnormal positioning of 1 or more of the calves within the birth canal. Conversely, the heavier BW of single calves increased the need for mechanical extraction to manage the dystocia. Likewise, the heavier male than female calves from single or bilateral twin births had a greater incidence of dystocia as well as a longer gestation length. Also, unilateral twins had a lighter birth weight and less dystocia in the fall than spring whereas birth weight and dystocia did not differ between seasons for single births. The Twinner cattle are large-type cattle, and single births have a greater incidence of dystocia relative to other cattle populations at USMARC. Estimated genetic correlations between birth or yearling BW and ovulation or twinning rate were positive (Gregory et al., 1997), and thus, selection for increased ovulation and twinning rate has further contributed to the increased calf size and dystocia. Current selection criteria include an emphasis to reduce birth weight for the population as well as to further assess the relationship between BW and twinning and possible antagonistic effects of such selection on future ovulation and twinning rates.

The male:female sex ratio (i.e., 0.52:0.48) for calves born in the Twinner population was similar to the sex ratio reported for other cattle populations (Foote, 1977) and did not differ from the theoretical 1:1 ratio. Furthermore, the sex ratio was the same for single and twin births and for unilateral and bilateral twins; thus, in utero survival of fetuses of 1 sex did not affect survival of the other sex. Published results (Martinez et al., 2004) are conflicting as to whether the sex ratio for calves is affected by length of interval between insemination and ovulation, early insemination at estrus (i.e., longer interval) resulting in more female than male calves. Twin preovulatory follicles were found to be about 3 mm smaller in diameter at AI than single preovulatory follicles but the variance was similar for the 2 ovulatory groups and the smaller diameter was not linked to timing of ovulation (Echternkamp et al., 2006a).

Greater than 95% of the females born cotwin or -triplet to a male(s) exhibit characteristics of the freemartin syndrome and are infertile (Gregory et al., 1996). Thus, only females born cotwin to a female are potential replacement heifers, which is sometimes thought to be a constraint to the utilization of twinning in beef cattle production. However, the total number of fertile female progeny produced by same-sex female twin births, which constitute 25% of the total twin births, is approximately equal to the total number of female progeny produced in a herd of single births. Because these twin females are full siblings, the genetic base of the pool of replacement females may be reduced to a small extent.

Results from the Twinner population at the USMARC confirm experimental results (Guerra-Martinez et al.,

1990; Gregory et al., 1996) that the production of twin births has the propensity to increase reproductive efficiency in beef cattle by 20 to 30%. However, a portion of the potential gain from twinning in cattle is compromised by reduced calf survival at birth, lighter BW of twin progeny at birth and weaning, and an increased incidence of dystocia associated with abnormal presentation of twin fetuses within the birth canal (Gregory et al., 1996; Echternkamp and Gregory, 1999). Also, the continued selection for an increased frequency of twin ovulations and births has increased the frequency of triplet ovulations and births, but triplet births provide little additional production benefits compared with twin births.

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